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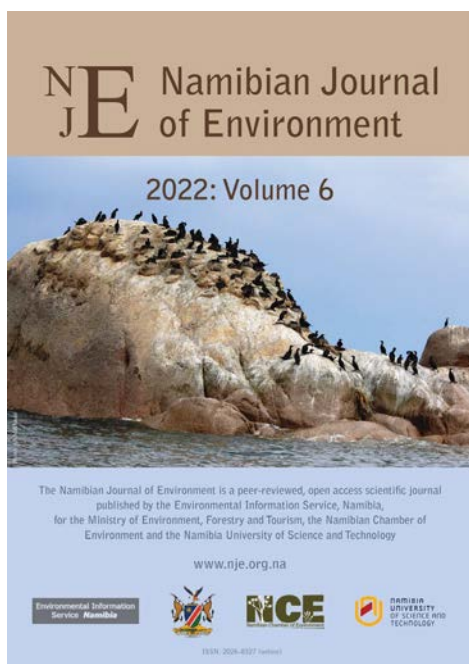
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SECTION A: RESEARCH ARTICLES

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Food limitation of seabirds in the Benguela ecosystem and management of their prey base

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ABSTRACT

Four of seven seabirds that are endemic to the Benguela ecosystem (African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis*, Cape Cormorant *Phalacrocorax capensis*, Bank Cormorant *P. neglectus*) compete with fisheries for prey and have an IUCN classification of Endangered. Prey depletion and food resource limitations have been major drivers of recent large population decreases of each of these species. As populations decrease, colony sizes also dwindle rendering them susceptible to Allee effects and higher probabilities of extinction. Therefore, it is necessary to maintain colonies at sizes that minimise their probability of extinction. Means to ensure an adequate availability of food to achieve this goal include closing important seabird foraging areas (often adjacent to key colonies) to relevant fishing, implementing ecosystem thresholds below which such fishing is disallowed (which are also expected to benefit forage resources) and, should there be an altered distribution of prey, attempting to establish seabird colonies close to the new location of forage resources.

Keywords: Allee effects; Benguela seabirds; conservation thresholds; food limitation; Namibia; spatial management

INTRODUCTION

This paper provides a brief review of food limitation of four Endangered (EN) seabirds that breed in the Benguela ecosystem, of the viability of seabird colonies and Allee effects, of forage and consumption thresholds and of potential management interventions that may enhance food availability. The locations of some of the system's important seabird colonies are shown in Figure 1.

STATUS OF THE BENGUELA'S SEABIRDS

Fifteen seabird species breed in the cool Benguela ecosystem, which extends from about Benguela in Angola to Woody Cape in South Africa, being bounded in the north and southeast by the warm Angola and Agulhas Currents, respectively (Figure 1). Seven of these are endemic to the ecosystem (Hockey *et al.* 2005). Of the endemic species, in terms of criteria of the International Union for Conservation of Nature (IUCN) four are EN

(African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis*, Cape Cormorant *Phalacrocorax capensis*, Bank Cormorant *P. neglectus*), one is Near-Threatened (NT, Crowned Cormorant *Microcarbo coronatus*) and two are Least Concern (LC, Damara Tern *Sternula balaenarum* and Hartlaub's Gull *Larus hartlaubii*, IUCN 2021). The non-endemic Leach's Storm Petrel *Hydrobates leucorhous* (or *Oceanodroma leucorhoa*) is Vulnerable (VU), whereas the other seven non-endemics are LC (IUCN 2021). Although substantial numbers of Leach's Storm Petrel migrate from the Northern Hemisphere into the Benguela system (Pollet *et al.* 2019), the breeding population of this species in South Africa is Critically Endangered (CR), as is that of Damara Tern (Taylor *et al.* 2015). In South Africa small, isolated populations of Great White Pelican *Pelecanus onocrotalus*, Caspian Tern *Hydroprogne caspia* and Roseate Tern *Sterna dougallii* are regarded as regionally VU (Taylor *et al.* 2015). Leach's Storm Petrel and Roseate Tern do not breed in Namibia, where Cape Gannet is considered CR

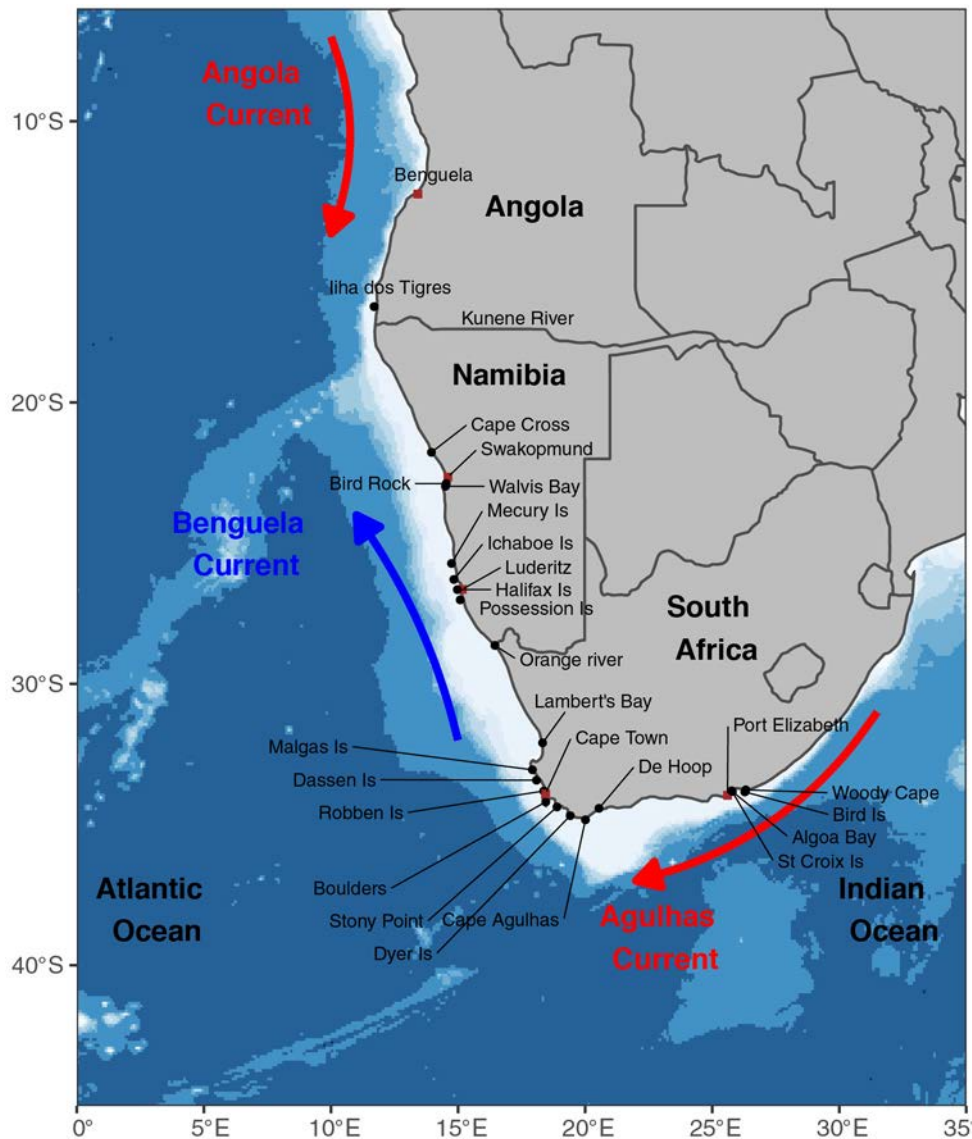


Figure 1: A map of the Benguela Current ecosystem showing locations of some of the region's important seabird breeding colonies and other localities mentioned in the text.

(Kemper 2015), Great White Pelican and Caspian Tern VU (Simmons 2015a, b) and Damara Tern NT (Simmons *et al.* 2015).

IMPORTANCE AND EVIDENCE OF FOOD LIMITATION

For a seabird population to be self-sustaining, mortality from its mature component must be balanced by recruitment or immigration. Recruitment is influenced by age at first breeding, breeding participation (proportion of mature birds electing to breed), breeding frequency (number of clutches produced annually), breeding success (chicks fledged per clutch) and survival from fledging to breeding. Insufficient food resources may negatively affect these demographic parameters leading to population

decreases, as is described below for the Benguela's four EN seabird species, which all feed mainly on three forage resources that are heavily exploited by fisheries when these are readily available. African Penguin, Cape Gannet and Cape Cormorant feed preferentially on sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Hockey *et al.* 2005). In South Africa, the intensively fished West Coast rock lobster *Jasus lalandii* is an important prey of Bank Cormorant (Dyer *et al.* 2019), whereas in Namibia the lightly-exploited but nutritionally-deficient bearded goby *Sufflogobius birarbatius* is one of its staple foods (Ludynia *et al.* 2010a). After the collapse of sardine in Namibia in the 1970s, bearded goby also replaced it as the dominant prey item for African Penguins breeding in Namibia (Ludynia *et al.* 2010b).

African Penguin

Large decreases of African Penguins at colonies between Lüderitz in Namibia and Dassen Island off west South Africa from the 1960s to the 1980s were recorded following the collapse of sardine stocks off Namibia and South Africa. North of Lüderitz, increases at Mercury and Ichaboe islands after the 1960s probably resulted from an increased local abundance of bearded goby (Crawford and Shelton 1978, Shelton *et al.* 1984, Crawford *et al.* 1985, 2001a). However, this did not prevent an overall decrease of 90% in penguins breeding in Namibia between 1956 and the early 2000s (Figure 2, Crawford 2007).

By contrast, an increase between the 1950s and 1970s and a later decrease in numbers of penguins at Dyer Island, southwest South Africa, coincided with an increase and subsequent fluctuations in anchovy abundance (Crawford 1998). From 1989–2009 numbers of penguins breeding along west South Africa were significantly correlated with the overall biomass of sardine and anchovy in South Africa, as also was the case from 1999–2009 in Algoa Bay (Figure 2, Crawford *et al.* 2011). The formation of new penguin colonies at Stony Point and Boulders on South Africa's mainland and at Robben Island, and increases at these colonies and at Dassen Island, took place during a period of recovery of South Africa's sardine in the 1980s and 1990s and an increase in the biomass of anchovy at the start of the 21st century. This led to an overall increase in the numbers of penguins breeding in west South Africa (Underhill *et al.* 2006).

After 2004, large decreases in numbers of penguins breeding in west South Africa were associated with a shift to the south and east of adult anchovy and sardine and a collapse of sardine (Crawford *et al.* 2011). Concomitant with the altered distribution of prey there were decreases in penguins at all South African colonies north of Cape Town (the northernmost colony at Lambert's Bay became extinct in 2006; Crawford *et al.* 2013). By contrast, in the south numbers increased or stabilised

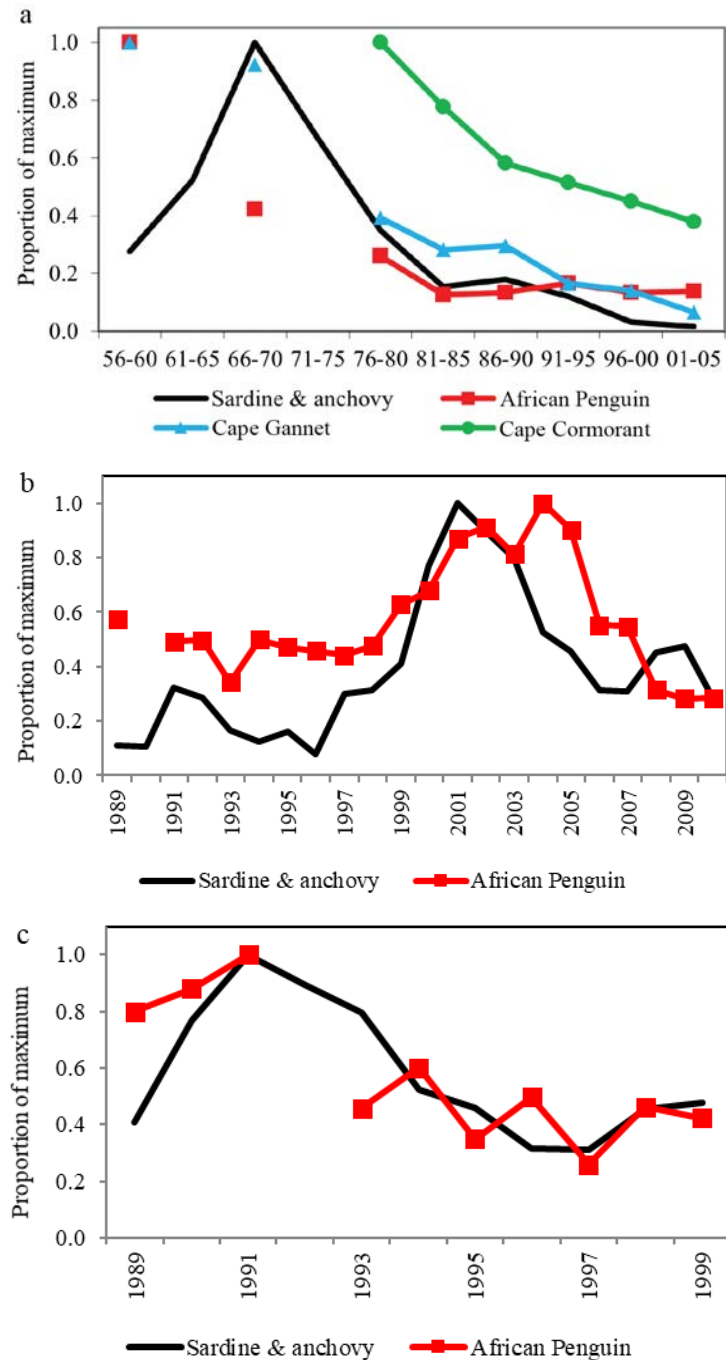


Figure 2: Comparison of trends in standardised estimates (maximum = 1) of the combined biomass of sardine and anchovy and breeding populations of seabirds that feed on these forage species for (a) Namibia 1956/60–2001/05 (redrawn from information in Crawford 2007), (b) west South Africa 1989–2010 and (c) Algoa Bay 1999–2009 (redrawn from information in Crawford *et al.* 2011). For west South Africa and Algoa Bay fish estimates are for the whole of South Africa.

at Boulders and Stony Point and penguins attempted to form a new colony at De Hoop Nature Reserve (Underhill *et al.* 2006, Crawford *et al.* 2011). Although trends in numbers of African Penguins at colonies are often regionally coherent (Underhill *et al.* 2006), at Dyer Island, also in the south, penguins

decreased in the 2000s. This may have resulted from heavy exploitation of sardine in its vicinity: 70,000 tonnes of sardine were caught within 30 km of Dyer Island in 2004 (Ludynia *et al.* 2014) and the exploitation rate of sardine west of Cape Agulhas increased to 30–44% in 2002 and from 2005–2007 (Coetzee *et al.* 2008). When the colony size at Dyer Island was > 3,500 pairs, numbers of penguins breeding there were negatively related to sardine catches made within 20 nautical miles of the island (Ludynia *et al.* 2014), suggesting an impact of catches on local food availability.

Local or regional abundances or availability of sardine and anchovy have been related to numbers of African Penguins breeding (Crawford 2007, Crawford *et al.* 2011, Sherley *et al.* 2013), to adult and immature survival (Crawford *et al.* 2011, 2019, Sherley *et al.* 2014, Robinson *et al.* 2015), to age at first breeding (Whittington *et al.* 2005), to breeding participation (Crawford *et al.* 1999b, Durant *et al.* 2010), to breeding success (Adams *et al.* 1992,

Crawford and Dyer 1995, Crawford *et al.* 1999b, 2006a, Cury *et al.* 2011, Sherley *et al.* 2013) and to foraging performance (Pichegru *et al.* 2010, 2012, Campbell *et al.* 2019, McInnes *et al.* 2019). Additionally, onset of breeding was probably delayed during a period of food scarcity (Crawford and Dyer 1995) and the chick fledging period was negatively correlated with prey abundance (Sherley *et al.* 2013). Delayed breeding and longer fledging periods may reduce the breeding frequency and cause abandonment of unfledged chicks when parents are constrained to leave colonies for pre-moult fattening (Crawford *et al.* 2018).

Cape Gannet

In Namibia, the Cape Gannet population decreased by 95% after the collapse of that country's sardine stock in the 1970s (Figure 2, Crawford 2007). However, at the same time the numbers of gannets in South Africa increased. Trends in the proportions of forage fish (sardine and anchovy) and gannets found

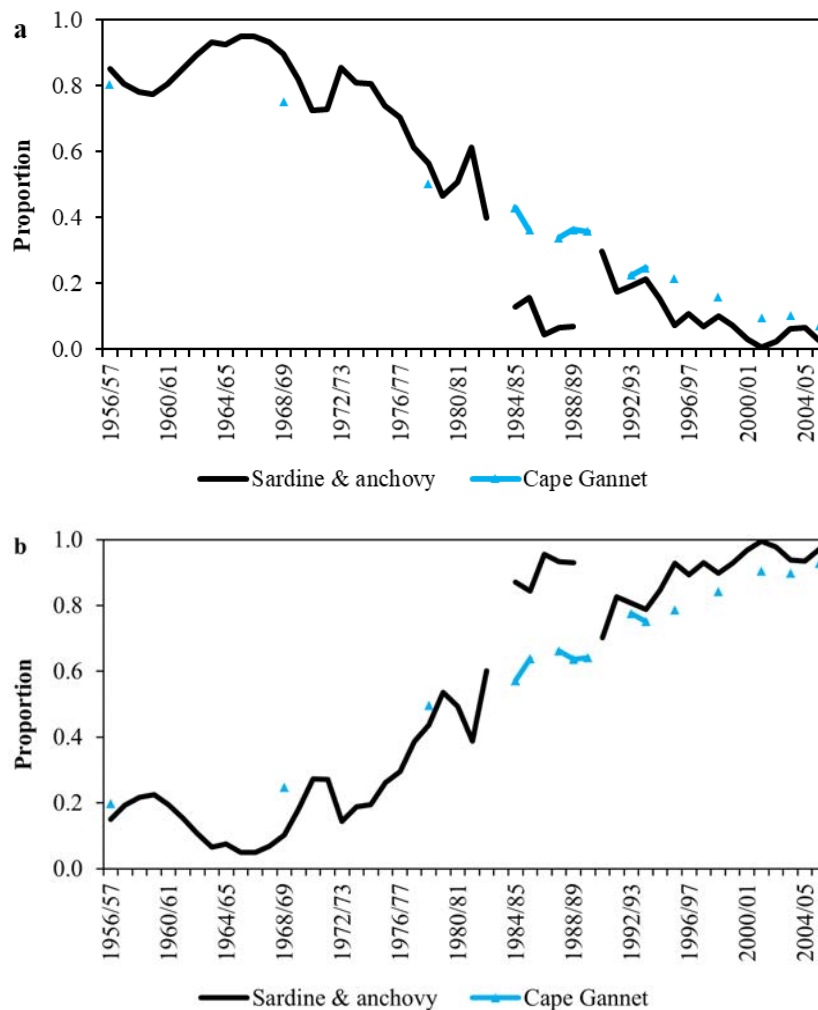


Figure 3: Trends in the proportions of the Benguela ecosystem's sardine and anchovy and Cape Gannet found in a) Namibia and b) South Africa, 1956/1957–2005/2006 (redrawn from information in Crawford *et al.* 2007a).

in Namibia and in South Africa were similar (Figure 3) suggesting an impact of food. However, increases of gannets in South Africa did not offset losses in Namibia so that the overall abundance of Cape Gannets decreased (Crawford *et al.* 2007a).

In the 21st century, the movement of Cape Gannets to the south and east continued with a decrease in numbers breeding off west South Africa and an increase in Algoa Bay, matching a shift in the distribution of their prey (Crawford *et al.* 2015, Sherley *et al.* 2019). In the west, foraging effort of Cape Gannets increased and nest attendance decreased with reduced consumption of sardine and anchovy, and adult body condition was negatively impacted by increases in the dietary proportion of hake *Merluccius* sp. discarded by fisheries (Cohen *et al.* 2014). At Malgas Island, Cape Gannets had substantially reduced breeding success when they fed their chicks mainly low-quality fish discards (Grémillet *et al.* 2008). Between 2011 and 2014 there was a net deficit in energy expenditure during foraging for most Cape Gannets tracked from Malgas Island (Grémillet *et al.* 2016).

Cape Cormorant

In Namibia, numbers of Cape Cormorants decreased by 62% after the collapse of sardine in the 1970s (Figure 2). It was a lesser decrease and occurred later than those of African Penguins and Cape Gannets, possibly owing to Cape Cormorants benefitting from increased breeding space at Ichaboe Island and making use of alternative prey in the form of bearded goby (Crawford 2007, Crawford *et al.* 2007b, Erasmus *et al.* 2021). Additionally artificial nesting platforms constructed in central Namibia provided breeding habitat for Cape Cormorants closer to the reduced range of the sardine (Crawford 2007). By contrast, gannets and most penguins in Namibia bred in the south and suffered food shortages as the sardine's range contracted northwards (Crawford 2007). Cape Cormorants colonised Ilha dos Tigres in southern Angola in the 2000s and > 16,000 pairs bred there in 2017 (Mendelsohn and Haraes 2018).

Unlike in Namibia, numbers of Cape Cormorants breeding in west South Africa decreased in the mid-1990s prior to recent decreases in that region of African Penguins and Cape Gannets (Crawford *et al.* 2007b). There were substantial mortalities of adult Cape Cormorants at several colonies in west South Africa between 1991 and 2006 caused by avian cholera *Pasteurella multocida*, outbreaks of which may be triggered by stressful events such as food limitation (Crawford *et al.* 1992a, Ward and Williams 2004, Waller and Underhill 2007). The initial occurrence of avian cholera at Dassen Island may have been precipitated by a scarcity of forage fish during 1989 and 1990 (Crawford *et al.* 1992a).

Conforming to the recent shift in the distribution of sardine and anchovy, Cape Cormorants decreased off northwest South Africa but remained stable in the south, where new colonies formed (including at Robben Island and Stony Point) and some others increased (Crawford *et al.* 2016).

When food is scarce, as well as experiencing increases in adult mortality, Cape Cormorants, like some other cormorant species, often skip or abandon breeding or delay their first breeding attempt (Berry 1976, Crawford *et al.* 2001b, 2016, Crawford and Dyer 1995). They may also suffer extensive breeding failure (Duffy *et al.* 1984, Crawford *et al.* 1992b). In November 2008, Cape Cormorants brooding small chicks expended significantly greater foraging effort at Malgas and Dassen islands than at Dyer Island farther south (Hamann *et al.* 2012). During May and June 2014 Cape Cormorants north of Cape Town attempted to take bait from hand-lines used to fish for snoek *Thyrsites atun*, a behaviour not previously observed and that suggested poor food availability at that time (Crawford *et al.* 2016).

Bank Cormorant

In Namibia, Bank Cormorants decreased from 7,166 pairs in 1978–1980 to 3,735 pairs in 1995–1997; a severe reduction of bearded goby in central Namibia in 1994 was a probable cause of the decrease (Crawford *et al.* 1999a). In South Africa, Bank Cormorants decreased from 1,506 pairs in 1978–1980 to 846 pairs in 2010–2013 (Crawford *et al.* 2015). Total numbers breeding at 11 readily accessible localities between Lambert's Bay and Dyer Island fell from above 500 pairs during 1978–1987 to 350 pairs from 1995 to 2006. The most northern colony (Lambert's Bay) was extinct by 1999 and there were substantial decreases at the two largest colonies, Malgas and Dassen islands, which are north of Cape Town. There was fluctuating growth at Robben Island, near Cape Town, where birds were oiled by spills in 1994 (*Apollo Sea*) and 2001 (*Treasure*). Farther east numbers at two colonies increased. These trends are consistent with a reduced abundance of rock lobsters in the north and an expansion of this resource to the east (Crawford *et al.* 2008). As with other endangered species, fishing in the immediate vicinity of Malgas and Dassen islands may have reduced densities of lobsters below levels needed to sustain the larger colonies of Bank Cormorants. Where rock lobsters had not been severely depleted, Bank Cormorants showed a positive response to their local availability and modelling suggested that areas with no-take of lobsters at 20–30 km around Bank Cormorant colonies would benefit the conservation of this seabird (Sherley *et al.* 2017).

COLONY VIABILITY AND ALLEE EFFECTS

Traditionally, the Benguela's four Endangered seabirds bred in large colonies and those three that feed mostly on sardine and anchovy have often foraged in large multi-species flocks (Hockey *et al.* 2005). However, as populations have fallen, breeding colonies have decreased in size and on occasion fragmented into smaller units (e.g. Cordes *et al.* 1999, Crawford *et al.* 2016, Sherley *et al.* 2019).

The probabilities of extinctions of different-sized colonies of African Penguins over 40 years were obtained from empirical observations on the performance of 41 discrete colonies in southern Namibia from 1956–1996 (Crawford *et al.* 2001a). Only one (< 4 %) of 28 colonies that in 1956 had ≤ 50 pairs was extant in 1996, compared to 26% of those having 251–1,000 pairs, 67% of those having 1,001–5,000 pairs and 100% of those with > 5,000 pairs (Figure 4). Whereas three of the 30 breeding colonies extant in 2004 held > 5,000 pairs and, in terms of these probabilities, had no likelihood of extinction within 40 years, by 2019 none of the 25 remaining colonies had > 5,000 pairs so that all had some chance of extinction during such a period. In

2019, fifteen colonies had < 250 pairs and hence a 96% chance of extinction by 2059 (Figure 4). In 2019, only seven colonies held > 1,000 pairs and had a 67% probability of surviving to 2059: Mercury Island in Namibia; Dassen, Robben, Dyer, St Croix and Bird (Algoa Bay) islands and Stony Point in South Africa.

Fragmented seabird populations may suffer from Allee effects, i.e. reduced fitness at low population size increasing their likelihood of extinction (Ryan *et al.* 2012). African Penguins that feed in groups have a higher catch of prey per unit effort than solitary birds (McInnes *et al.* 2017), but colonies may become too small for sufficient foraging groups to form (Ryan *et al.* 2012). For example, in 2012 more penguins were documented foraging in a single flock of at least 158 birds (Ryan *et al.* 2012) than were breeding in 2019 at 10 of the 25 presumed extant African Penguin colonies. For plunge-diving Cape Gannets, highly-synchronised prey pursuits, which are likely contingent on their ability to locate an adequate number of conspecifics at sea, benefitted foraging efficiency when feeding on sardine schools (Thiebault *et al.* 2016). A lower number of individuals could also decrease the role of colonies as

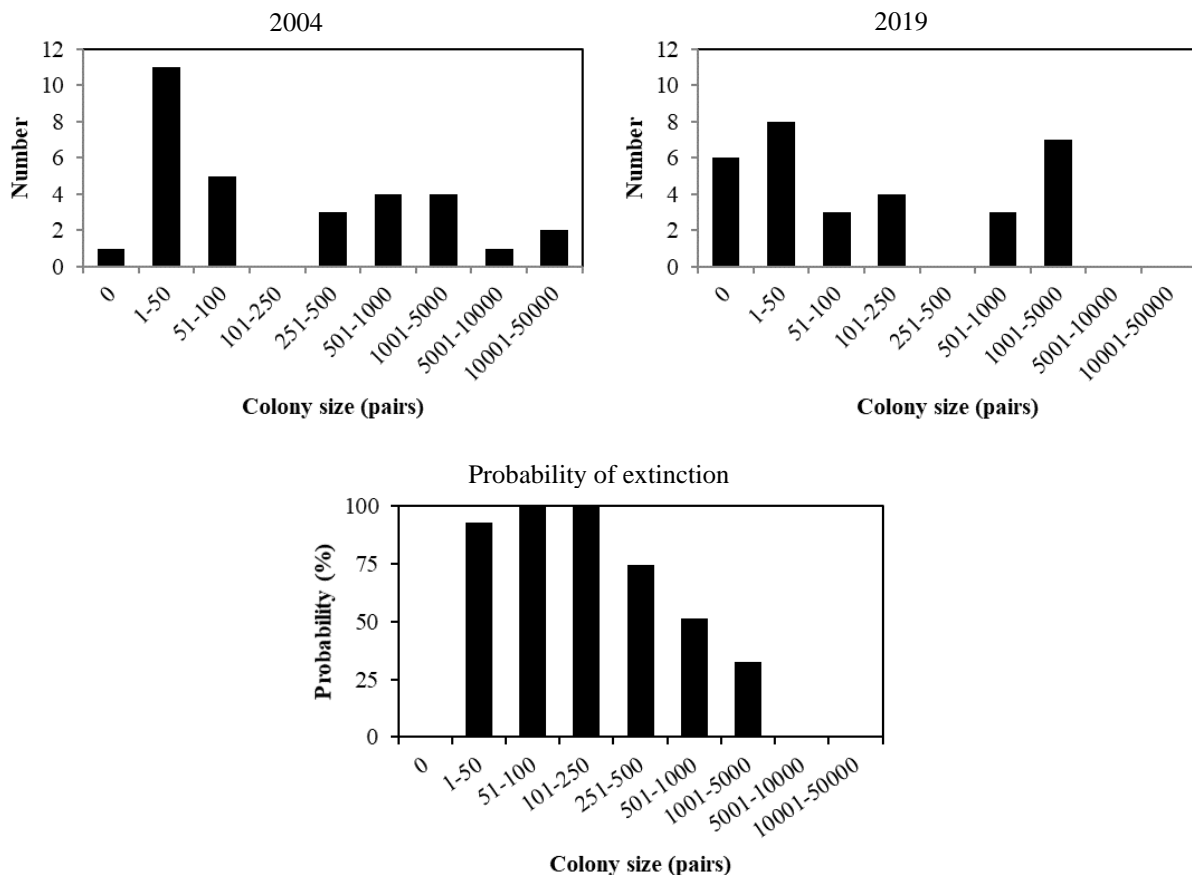


Figure 4: Top: numbers of African Penguin colonies of different sizes in 2004 (left) and 2019 (right). Numbers of colonies where breeding occurred since 1956 that were extinct in 2004 and 2019 are indicated by colony size = 0. Bottom: probabilities of extinction over a 40-y period of African Penguin colonies of different sizes derived from empirical information in Crawford *et al.* (2001a).

information centres, or the possibility to use conspecifics as cues to locate prey (e.g. Thiebault *et al.* 2016). Again smaller colonies have a larger proportion of birds nesting at colony edges, where eggs and chicks are at a greater risk to predation (e.g. Cordes *et al.* 1999), and sex-biased mortality (e.g. Pichegru and Parsons 2014) may decrease productivity of monogamous breeders at small colonies. The higher risks of extinction for small colonies make it imperative to maintain colony sizes above thresholds at which Allee effects are manifest. Furthermore, seabirds that have a late age at maturity may take substantial periods to recover from small numbers, even with fishery closures (e.g. Robinson *et al.* 2015).

In 2010, Mercury Island held 72% of the global population of Bank Cormorants (Roux and Kemper 2015) and 73% of Namibia's African Penguins (Crawford *et al.* 2013). In 2018, c. 70% of the overall Cape Gannet population was at Bird Island, Algoa Bay at the eastern boundary of the Benguela ecosystem (Sherley *et al.* 2019). In the 2010s, 54% of South Africa's Cape Cormorants bred at Dyer Island (Crawford *et al.* 2016). Such congregations of large proportions of a species at a single locality may offset allee effects but render the species highly susceptible to local catastrophic events such as oil spills (e.g. Crawford *et al.* 2000), disease outbreaks (e.g. Waller and Underhill 2007), severe weather events (e.g. Randall *et al.* 1986) and reduced availability of resources.

FORAGE THRESHOLDS

Forage abundance thresholds

In a meta-analysis of long-term studies in seven marine ecosystems from around the globe, Cury *et al.* (2011) demonstrated key thresholds in prey (fish and krill) abundance, below which seabirds dependent on that food type suffered reduced and more variable breeding productivity. The threshold was equal to the long-term average biomass of prey and equivalent to one-third of the maximum observed prey biomass. Similar relationships were established for 13 of the 14 seabirds studied, including African Penguin and Cape Gannet from the Benguela ecosystem. The so-called "1/3 for the birds" rule provides a benchmark for management of forage fish fisheries at a level that would sustain seabird productivity over the long-term (Cury *et al.* 2011).

In a related study, Robinson *et al.* (2015) showed that annual mortality of adult African Penguins at Robben Island increased markedly when the biomass of sardine aged 1 y or older off west South Africa fell below 25% of its maximum value. The lower forage threshold observed for adult mortality (25%) than for breeding success (33%) confirmed the theoretical

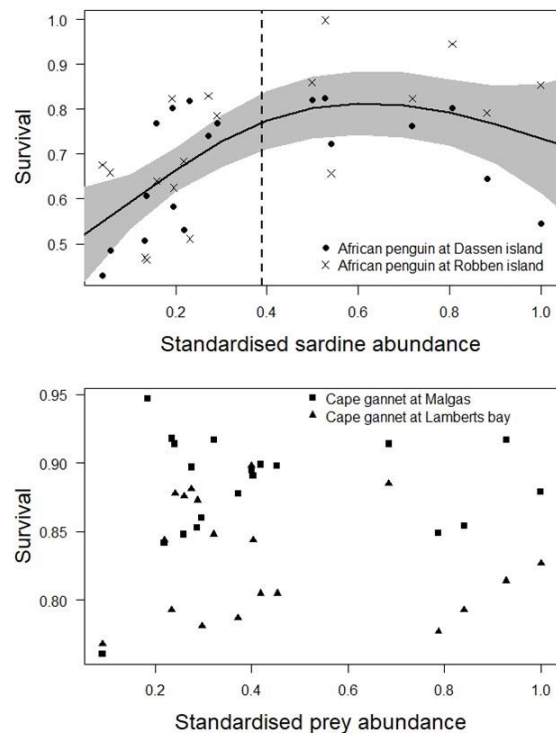


Figure 5: Estimated adult survival off west South Africa of (top) African Penguins at Dassen Island and Robben Island and (bottom) Cape Gannets at Lambert's Bay and Malgas Island compared with the standardised abundance of prey off west South Africa (i.e. centred and scaled by dividing by the standard deviation). Estimates of survival were from Sherley *et al.* (2014) for African Penguins and Distiller *et al.* (2012) for Cape Gannets. Estimates of prey abundance were updated from Cury *et al.* (2011). The prediction (and 95% confidence interval) of the GAM is indicated with the black curve (and grey polygon) for African Penguins. The vertical dashed line represents the threshold below which adult survival decreased markedly with decreasing sardine abundance. For Cape Gannets, no significant relationship was found between adult survival and prey (sum of anchovy and sardine) abundance.

prediction of Cairns (1987) that decreases in forage abundance would influence seabird breeding success ahead of survival. When data for African Penguins at Dassen and Robben islands were grouped, a generalised additive model (GAM) showed that adult survival decreased when standardised (i.e. centred and scaled) sardine abundance off west South Africa fell below a threshold of zero (Figure 5).

It is noteworthy that off west South Africa, Cape Gannets were better able to buffer effects of reduced prey abundance than African Penguins (Distiller *et al.* 2012, Sherley *et al.* 2014, Robinson *et al.* 2015). After an eastward displacement of the main forage resources and the collapse of sardine (Coetzee *et al.* 2008), adult gannets, due to their movement capabilities, were able to feed on alternative food,

such as saury *Scomberesox saury* and hake offal (Grémillet *et al.* 2008, 2019, Crawford *et al.* 2014, 2019). Consequently, their survival was unrelated to standardised estimates of the overall abundance of sardine and anchovy (Figure 5).

Forage consumption thresholds

Saraux *et al.* (2021) investigated thresholds for the consumption of forage fish stocks by seabirds in five marine ecosystems: off Norway, South Africa, Peru, in the Baltic Sea (Sweden) and at Shetland (Scotland). In each of these systems, the predation pressure, estimated as the proportion of a forage fish stock consumed by seabirds, was generally small (median = 1% of biomass) but increased sharply when prey biomass decreased below a threshold of 15 to 18% of its maximum recorded value. A threshold of 18% was considered a limit not to be reached in order to avoid a sharp rise in the natural mortality rate of forage fish resources, and below which extra cautious management of fisheries would be required (Saraux *et al.* 2021). Similarly, Essington *et al.* (2015) advised that a risk-based management scheme that reduces fishing when populations become scarce would protect both forage fish and their predators from collapse, with little effect on long-term average catches.

OTHER FORAGE CONSIDERATIONS

Forage quality

Condition of prey may influence its ability to sustain predator populations in addition to its abundance (e.g. Grémillet *et al.* 2008). For example, poor food quality likely caused unprecedented breeding failures at many seabird colonies on the east coast of Great Britain in 2004 (Wanless *et al.* 2005), decreased mass at fledging of Common Guillemots (Murre) *Uria aalge* in the Baltic Sea and brought about breeding failures and mass mortality of this species in the Northeast Pacific in 2015–2016 (Osterblom *et al.* 2006, Piatt *et al.* 2020). In South Africa, the condition of sardine deteriorated in the 2000s (Ndjaula *et al.* 2013), possibly contributing to some of the seabird population decreases. As also mentioned above, reliance on fish offal as a food source reduced Cape Gannet chick survival (Grémillet *et al.* 2008).

Fisheries mortality

In addition to contributing to collapses of forage resources (e.g. Essington *et al.* 2015), fishing may cause localised depletion of prey; as such, the fisheries mortality rate (F) can be employed as another management threshold. For example, the performance of three species of *Pygoscelis* penguins breeding near the Antarctic Peninsula was reduced when local harvest rates of Antarctic krill *Euphausia*

superba were $\geq 10\%$ of the estimated biomass (Watters *et al.* 2020). By comparison, the exploitation rate of South Africa's sardine west of Cape Agulhas increased substantially after 1999 and reached 44% in 2006 (Coetzee *et al.* 2008). Spatially explicit thresholds in fishing mortality need to be carefully defined to assist in management of fish stocks so as to support viable seabird populations in the Benguela system.

Forage availability

It is not only the absolute abundance of prey but also its availability that impacts energy acquisition, demography and population trends of seabirds. For example, Crawford *et al.* (2019) used long-term information on the diet of Cape Gannets off west South Africa to derive an index of the availability of anchovy and sardine per unit biomass to seabirds in that region, terming it a Forage Availability Index (FAI). The study demonstrated a substantial decrease in the availability of anchovy and sardine to seabirds in the 2000s compared to the 1990s. Breeding numbers of Cape Gannets and Cape Cormorants and survival of adult African Penguins at both Dassen and Robben islands were significantly related to the FAI. For gannets, the numbers breeding increased when the FAI, which increases as anchovy and sardine contribute more to the diet, was $> c. -1$ and for cormorants when it was $> c. 1$. The higher threshold for Cape Cormorants than Cape Gannets at which numbers breeding were predicted to increase probably resulted from the fact that, unlike Cape Gannets but similarly to African Penguins, Cape Cormorants are mostly unable to access alternative food such as saury and hake offal (Crawford *et al.* 2019). Notably, frequent aggregations of anchovy close to the seabed were thought to have reduced their availability to purse-seiners, and were suggested as a reason for a large under-catch of the total allowable catch (TAC) of anchovy in recent years (DAFF 2016).

The importance of prey depth was highlighted in a modelling study from the Humboldt upwelling system off western South America, where it primarily determined foraging success of Peruvian Boobies *Sula variegata* and Guanay Cormorants *P. bougainvillorum*, which feed mainly on Peruvian anchoveta *Engraulis ringens* (Boyd *et al.* 2017). Peruvian Boobies and Guanay Cormorants are the ecological equivalents in that system of Cape Gannets and Cape Cormorants in the Benguela system (Crawford *et al.* 2006b).

African Penguins and other diving piscivores may herd prey shoals upwards, thereby facilitating their availability to surface-feeding predators (e.g. McInnes and Pistorius 2019). Hence their loss will influence ecosystem functioning.

POSSIBLE INTERVENTIONS TO ENHANCE FOOD AVAILABILITY

Various international agreements require participating parties to implement an ecosystem-based approach to fisheries management (EAF). For example, the Code of Conduct for Responsible Fisheries of the United Nations' Food and Agriculture Organisation, adopted in 1995, stated that *Management measures should not only ensure the conservation of target species but also of species belonging to the same ecosystem or associated with or dependent upon the target species* (<http://www.fao.org/3/v9878e/v9878e00.htm>). The sixth Aichi Target of the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 reads: *By 2020 all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits* (<https://www.cbd.int/convention/text/default.shtml>). In South Africa, the Marine Living Resources Act of 1988 attempts to provide legislative support for the EAF but is in urgent need of updating and further amendment better to achieve this (Cochrane *et al.* 2015).

One tool available to manage fisheries so as to avoid harmful impacts on associated or dependent species (ADS) is marine spatial planning, for example the implementation of fishing closures around important seabird colonies (e.g. Ludynia *et al.* 2012, Sherley *et al.* 2015, 2018). In northeast Scotland, Black-legged Kittiwakes *Rissa tridactyla* benefitted from closure of fishing for sandeels *Ammodytes marinus*, an important prey for kittiwakes, around breeding colonies (Daunt *et al.* 2008, Furness 2020). In the Californian upwelling ecosystem off west North America, a precautionary ecosystem approach that avoids localised depletion of forage resources (including anchovy and sardine) near predator concentrations is deemed necessary. In 1983, nearshore (within 3 to 6 km of the coast) fishing for anchovy was prohibited, the main objectives being to protect pre-recruit anchovy, live bait and recreational fisheries, and predator forage (Pacific Fisheries Management Council 1983, Thayer and Sydeman 2020). At the time, the anchovy-dependent Brown Pelican *Pelecanus occidentalis* was listed as Federally Endangered in USA (Anderson *et al.* 1982). In the Humboldt upwelling ecosystem off west South America, fishing for Peruvian anchoveta close to a Peruvian Booby colony increased the birds' foraging effort. The more the fishery reduced the quantity of anchoveta in the area, the farther the

breeding boobies needed to forage from the colony to find food (Bertrand *et al.* 2012). In the Benguela system, in which similarly to the California and Humboldt systems sardine and anchovy are key forage resources, short-term fishery closures around African Penguin colonies, even though not matched to the late age at recruitment and high mate and site fidelity of the penguins (Crawford *et al.* 2013), have increased breeding productivity and decreased parental foraging costs (Pichegru *et al.* 2010, Sherley *et al.* 2015, 2018, Sydeman *et al.* 2021).

A second means to account for the foraging requirements of marine predators is the identification and implementation of ecosystem thresholds, below which fishing would be prohibited. Ecosystem thresholds have already been widely applied to minimise by-catch mortality of ADS in fisheries (e.g. Rollinson *et al.* 2017, Da Rocha *et al.* 2021) and are increasingly proposed as means to ensure sufficient quantities of prey for predators, such as seabirds (e.g. Cury *et al.* 2011, Smith *et al.* 2011, Sydeman *et al.* 2017, Hill *et al.* 2020). In the Californian upwelling ecosystem, a harvest rule disallows fishing of sardine when its biomass is below 150,000 metric tonnes (Pacific Fisheries Management Council 2003, Thayer and Sydeman 2020).

A third mechanism to achieve adequate food for seabirds is to offset mismatches in the distributions of the breeding localities and the prey of seabirds through establishment of colonies nearer to the food supply. Guano platforms in Namibia served this purpose for Cape Cormorants (Crawford 2007) and an attempt to establish a new African Penguin colony in South Africa closer to the present distributions of sardine and anchovy has been initiated (BirdLife South Africa 2016).

Recommendations from the 2020 AEWA Benguela Current Forage Fish Workshop

In November 2020, a *Benguela Current Forage Fish (BCFF) Workshop*, organised by the African-Eurasian Migratory Waterbird Agreement (AEWA), in collaboration with the Benguela Current Convention (BCC) and BirdLife South Africa, recommended actions to be undertaken as a matter of urgency under the auspices of BCC, AEWA and the AEWA Benguela Coastal Seabird International Working Group, as well as by the national governments of Angola, Namibia and South Africa. These included:

- developing tools to increase the availability of sufficient forage [fish] for threatened endemic Benguela seabird species, such as setting ecosystem thresholds (i.e. sizes of forage resource populations below which a range of precautionary measures relating to fishing would be implemented at various spatial scales)

and closing key foraging areas to fishing, adjacent to major seabird colonies;

- ensuring the existence or creation of suitable seabird breeding habitat within the contracted or altered distributions of forage fish species to partially alleviate the impact of an altered distribution of prey on affected seabird species;
- and facilitating and prioritising the recovery of seabird colonies to sufficient sizes to minimise known and potential Allee effects, thus reducing the probability of colony extinctions (AEWA 2020).

CONCLUSION

In conclusion, it is apparent that food limitation has been a major driver of adverse trends in the population sizes and conservation status of four Benguela seabirds that compete with fisheries for food. Hence it will be important to manage the impact of fisheries on the availability of prey to these seabirds, including through the use of measures that were successfully applied elsewhere or that have empirical support for use in the Benguela ecosystem.

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